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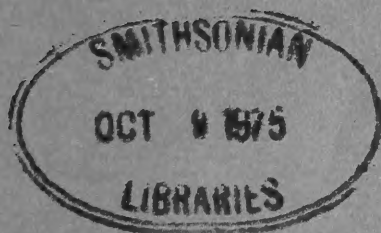
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# ANNALS

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- FISCHER, P.-H. 1948. Données sur la résistance et de la vitalité des mollusques.—*J. Conch.*, Paris 88: 100-140.
- FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Etudes sur les échanges respiratoires des littorines.—*Archs Zool. exp. gén.* 74: 627-634.
- KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon.—*Ann. Mag. nat. Hist.* (13) 2: 309-320.
- KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean.—*Bull. Bingham oceanogr. Coll.* 17 (4): 1-51.
- THELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* 4: 269-270. Jena: Fischer.—*Denkschr. med.-naturw. Ges. Jena* 16: 269-270.

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THERMALLY ANOMALOUS  
LATE PLEISTOCENE MOLLUSCS  
FROM THE SOUTH-WESTERN CAPE PROVINCE,  
SOUTH AFRICA

By

ANTHONY J. TANKARD

Cape Town

Kaapstad

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# THERMALLY ANOMALOUS LATE PLEISTOCENE MOLLUSCS FROM THE SOUTH-WESTERN CAPE PROVINCE, SOUTH AFRICA

By

ANTHONY J. TANKARD

*South African Museum, Cape Town*

(With 3 figures and 2 tables)

[MS. accepted 29 May 1975]

## ABSTRACT

Numerous exposures of Late Pleistocene marine sediments occur on the west and south coasts of the Cape Province. The mollusc fauna, which includes some 124 species, only 3 of which are extinct, lived in sediments deposited during the last interglacial. Two broad and contemporaneous facies are recognized: a cool-water open-coast facies, and a warm-water estuarine-lagoonal facies. Whereas the open-coast facies is characterized by molluscs which presently live on the adjacent coast, the estuarine-lagoonal facies regularly contains tropical species which lived far south of their known present-day geographic ranges. Differences in distribution between the fossil warm-water molluscs and their present-day temperature-sensitive counterparts have been used to interpret Late Pleistocene climatic change in the south-western Cape. These deposits are correlated with the Mediterranean Eutyrrhenian.

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## INTRODUCTION

Isolated fossiliferous, marine sediments occur on the wave-cut platform and in the sheltered Late Pleistocene embayments from Elands Bay on the west coast to Knysna on the south coast. The fossils occur in unconsolidated quartzose and shelly quartzose sands. The invertebrate fauna is essentially modern in composition and comprises some 150 species which today live in shallow-water environments. Only three of the mollusc species from the west

coast deposits are not known to be living today. In so far as most of these taxa are still living, and are inhabitants of shallow water, they provide ideal material for a palaeoecological study.

The Late Pleistocene fauna of the west coast is broadly divisible into two distinct, but contemporaneous, ecologic zones. These are, firstly, a cool-water, open-coast facies characterized by rocky shore and sandy beach assemblages, and secondly, a warm-water, sheltered embayment facies (estuaries and lagoons). Whereas the open-coast facies is laterally continuous, the sheltered embayment facies is restricted in distribution. The open-coast facies is characterized by molluscs which commonly inhabit the present coast. A striking feature of the estuarine-lagoonal facies is the association of extant and extralimital thermophilic species. ('Thermophilic' and 'extralimital' imply species which occur outside their normal spawning range.) Examination of their present latitudinal ranges indicates that a significantly warmer hydroclimate prevailed when those species were common along the south-western Cape coast. In attempting to reconstruct the palaeoenvironment, a detailed examination of a south coast assemblage is necessary. The fossiliferous deposits at Knysna are therefore included in the study.

Late Pleistocene faunas of open-coast and sheltered-embayment aspects from southern California are similarly distinctive. Nearly all the dominant species also inhabit the adjacent coast. But the sheltered embayments also contain a high proportion of thermophilic molluscs which are found far north of their present-day geographic range end-points. Several authors have used these anomalies as a key to Late Pleistocene climatic interpretation (Valentine 1955, 1957, 1961; Valentine & Meade 1961; Addicott & Emerson 1959; Emerson & Chase 1959; Kern 1971). Valentine (1955) explained the diverse nature of the fauna by changes in intensity of the oceanic circulation and upwelling, while the water of the embayments was heated by increased solar radiation. A recent alternative explanation suggests that the larvae of tropical molluscs were transported into the cooler areas by periodic local and temporary current changes, and that they became only temporary, non-breeding, members of the community (Zinsmeister 1974).

The south-western Cape Province, with its extensive Late Pleistocene fossiliferous deposits, and its complex present-day ocean current systems, is well placed to make a contribution to the knowledge of Late Pleistocene hydroclimates. The purpose of this paper is to describe the mollusc fauna, particularly between Ysterfontein and Elands Bay, and to examine their palaeoenvironmental significance. The taxonomy of some of these molluscs appears elsewhere (Kilburn & Tankard, in press).

### GEOLOGIC SETTING

The Pleistocene epoch was characterized by the waxing and waning of continental ice sheets with sea level oscillating in sympathy. Relative movement of sea level is shown by the emerged wave-cut platforms, stranded beaches,

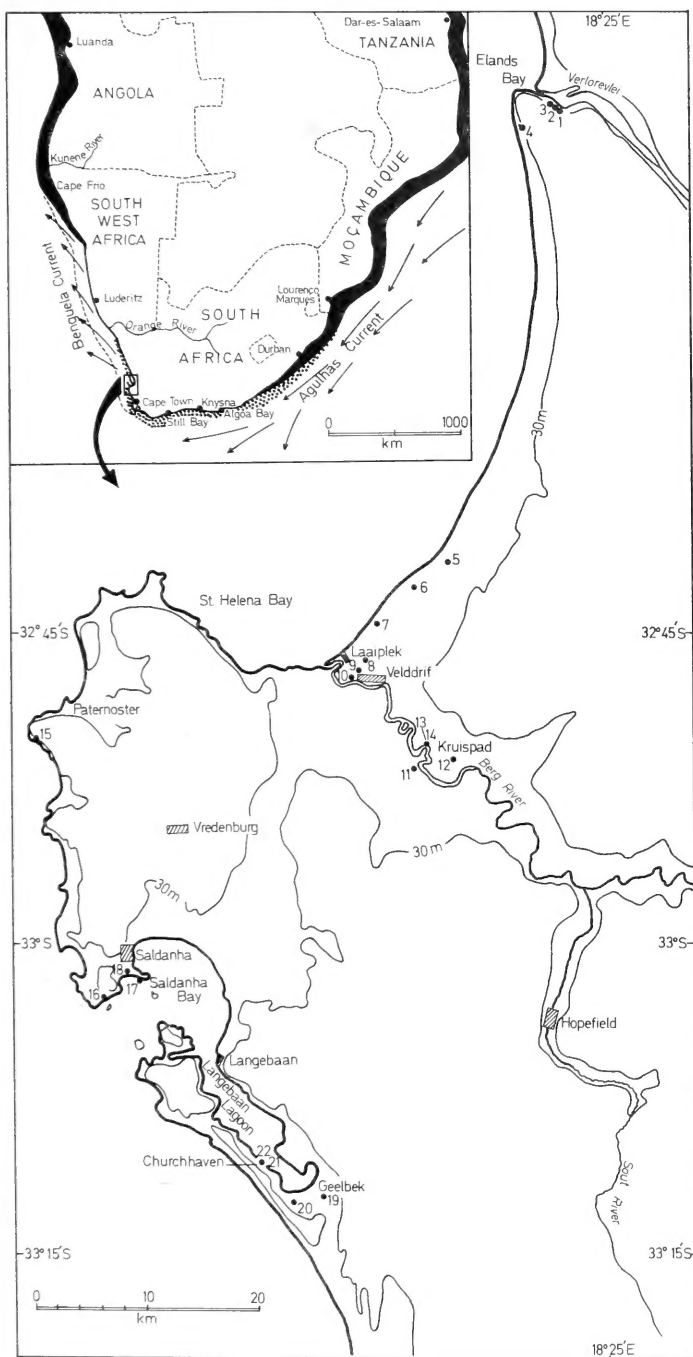


Fig. 1. Locality map. The insert (partly after Boss 1969) shows the distribution of present-day coastal forms: black = tropical; stippled = warm-temperate; area bounded by broken line on west coast = cold water fauna.

and marine terraces. Research on Barbados has suggested the existence of three transgressions in the last interglacial (Eem): +6 m (BI) at 122 ka (i.e. 122 000 years ago); -13 m (BII) at 103 ka; -13 m (BIII) at 82 ka (Broecker *et al.* 1968). These three peaks are confirmed by oxygen isotope studies of deep-sea cores (Shackleton & Opdyke 1973).

Along the west coast of South Africa a thin mantle of Late Pleistocene marine sediments overlies earlier Pleistocene, Tertiary, and pre-Tertiary rocks. On the granitic headlands between St. Helena Bay and Ysterfontein a narrow seaward-sloping wave-eroded platform is encountered. St. Helena Bay has formed on Malmesbury rock which weathers more rapidly than the granite and gives a negative relief. The open-coast fossil assemblages were collected from marine deposits overlying the granite platforms, and from exposures in the coastal flats bordering St. Helena Bay.

The last interglacial shorelines parallel the present coast very closely, with two exceptions. Whereas the present coastline is interrupted only by Saldanha Bay and its southerly offshoot, Langebaan Lagoon, the Late Pleistocene sea extended up the Berg River valley and along Verlorevlei to form two prominent estuaries. Verlorevlei is now separated from the sea by a bar of Palaeozoic sandstone at 1 m a.s.l. (above mean sea level). These sheltered Late Pleistocene estuaries and lagoons were of considerable palaeogeographic importance since all fossil sites within them contain a significant proportion of thermophilic mollusc species.

The greatest observed thickness of the open-coast facies exceeds 5 m at Velddrif; the greatest observed thickness of the estuarine facies is 2,2 m at Verlorevlei. The open-coast facies consists of medium-grained quartzose sand and comminuted shell. Frequently there are shell beds and banks with little detrital quartz, indicating a slow supply of detrital sediment. A series of emerged breaker-bars between Velddrif and Laaiplek parallel the modern coast. These are composed largely of shell material.

In all the sheltered embayments the fossils are found in fine sands. At Verlorevlei the marine horizon is overlain by coarse, poorly-sorted colluvium. At Churchhaven the marine sediments are carbonate cemented and form an erosional bench just above high-water level. Most of the sites examined, both open-coast and sheltered embayment, are covered with a veneer of wind-blown sand.

## METHODS

The absolute density of fossil specimens of each molluscan species at any particular site is difficult to determine because of the sampling problems inherent on the size of the shell. For instance, '*Rissoa capensis*' is a small gastropod (usually less than 3 mm) and would frequently number in the hundreds from just 100 g of sediment, while the large (approximately 200 mm) *Panopea glycymeris* would occur at approximately 1 m intervals. Bearing in mind that the present study is a palaeoecological one, and that the larger



molluscs have been better studied with respect to taxonomy and ecology, emphasis has in all cases been placed on the macro-molluscs. A further source of error arises from the differential fragmentation of shells. Bivalve shells are more easily broken than gastropod shells, and in the living assemblage they may have been far more abundant than the faunal list suggests. Table 1 should be taken only as an approximation to the original community structure.

The procedures adopted in drafting Table 1 are as follows:

1. It was desirable to sample as small an area as possible to obtain not only the absolute density of each species, but also to obtain restricted samples for size-frequency analyses. In most cases a quadrat size of 1 square metre has been found adequate, although quadrat size may have to be adjusted up or down depending upon the relative abundance of specimens.

2. For a shell to be counted as an individual it must be nearly complete, or so nearly so that the remainder could not be identified and counted separately. Left and right valves of each bivalve species were counted separately, and the highest count taken as the total number of individuals of that species in that quadrat.

3. Each species has been recorded in Table 1 as percentage frequencies in the sample where more than 50 individuals were counted. Where a total of less than 50 individuals were counted they are recorded in Table 1 as '×'.

No attempt has been made to relate species to sediment texture since every mollusc at some time must have been living among already dead and fragmented shells. The substrate would thus consist of quartzose sand and bioclastic material ranging in size from complete shells to finely comminuted fragments.

### PALAEOECOLOGY

In this paper past extensions of tropical and subtropical mollusc geographic ranges are used as a basis for interpreting Late Pleistocene palaeotemperature changes. These inferences are based only on fossils of still extant species, and the assumption (Durham 1950) that stenothermal organisms are in general more critically limited by minimum temperatures than by maximum temperatures. The validity of such palaeotemperature inferences depends on the fossils being preserved in the sediments in which they once lived.

In describing the relationship between the fossils, after death, and the sedimentary environment, we define the following types of fossil assemblages:

1. Life assemblage: disturbance after death negligible (Hallam 1960).
2. Death assemblage:
  - (i) Indigenous: organic remains disturbed after death but not transported very far (Hallam 1960).
  - (ii) Transported: organic remains introduced from a neighbouring contemporaneous or older environment.
3. Mixed assemblage: this comprises any combinations of the above





TABLE 1 (contd.)  
Distribution and Abundance (%) of Late Pleistocene Molluscs

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	Floor	Lagoon	Kayana
<b>BIVALVIA (contd.)</b>	9,0	20,0	26,4								8,0	15,4	×	×					20,4	14,1	< 1	4,1		57,5	1,4
<i>Loripes livatula</i> (Sowerby)																									
<i>Anodonta edentula</i> (Linnaeus)																									
<i>Felania diaphana</i> (Gmelin)																									
<i>F. subradiata</i> Sowerby								×																	
<i>Erycina subradiata</i> (Gould)																									
<i>Lasaea rubra</i> Montagu																									
<i>Myrella convexa</i> (Gould)																									
<i>Tellinina trigona</i> Barnard								×																	
<i>Tellinina</i> sp.																									
<i>Cardita</i> sp.																									
<i>Paricardium turtoni</i> (Sowerby)																									
<i>Macra glabrata</i> Linnaeus																									
<i>M. ovalina</i> Lamarck																									
<i>Scissodesma spengleri</i> (Linnaeus)																									
<i>Lutraria lutraria</i> (Linnaeus)																									
<i>Lutraria</i> sp.																									
<i>Solen capensis</i> Fischer																									
<i>Phaxas pellicidus</i> (Pennant)																									
<i>Tellina ponsanbyi</i> Sowerby																									
<i>T. madagascariensis</i> Gmelin																									
<i>T. trilatera</i> Gmelin																									
<i>T. gilchristi</i> Sowerby																									
<i>Macoma crawfordi</i> Sowerby																									
<i>M. litordis</i> (Krauss)																									
<i>M. tricostrata</i> (Römer)																									
<i>Gastrea matadoc</i> (Gmelin)																									
<i>G. fibrosa</i> Kilburn & Tankard																									
<i>Leporimetis hanleyi</i> (Dunker)																									
<i>Donax serri</i> (Chemnitz)																									
<i>D. sanctuarium</i> Kilburn & Tankard																									
<i>Psanmotellina capensis</i> Sowerby																									
<i>Theora alfredensis</i> Bartsch																									
<i>Venus verrucosa</i> Linnaeus																									
<i>Tivela tomlini</i> Haughton																									
<i>Dosinia lupinus</i> Linnaeus																									
<i>D. hepatica</i> (Lamarck)																									
<i>Venerupis senegalensis</i> Gmelin																									
<i>V. dura</i> Gmelin																									
<i>Panopea glycymeris</i> (Born)																									
Total number individuals	100	100	148	75					105		50	156		204	153		153	153	98	85	256	121		492	
% thermophilic species	60,0	75,0	26,1						26,1		22,2	25,8		33,0			6,9	26,9	31,6	31,6	22,6	25,9		12,8	
% thermophilic individuals	17,0	33,0	41,9						41,9		20,0	42,9					—	45,9	32,9	28,1	35,5			60,4	

possibilities, and is the general case (Hallam 1960). The status of this assemblage is clarified by describing it, for instance, as a mixed life and indigenous death assemblage. In the present study this is the commonest case.

#### POPULATION DYNAMICS

Boucot (1953), Olson (1957), Craig & Hallam (1963), and Craig & Oertel (1966) have attempted to discriminate between life and indigenous death assemblages on the one hand and transported death assemblages on the other, by using size-frequency distributions. According to Boucot an indigenous death assemblage is characterized by a positively skewed distribution (large number of small forms), while negative skewness or a normal distribution characterizes the transported death assemblage. He suggested that negative skewness resulted from winnowing of the smaller shells. Craig & Oertel (1966) question this and maintain that the shape of the size-frequency distribution in a fossil population depends principally upon the growth-rate and mortality-rate of the relevant species. In this way negative skewness could arise from a decreasing growth-rate with constant mortality-rate which would concentrate the older age-classes in a few size-classes. Craig and Oertel suggest the following options:

<i>Growth-rate</i>	<i>Mortality-rate</i>	<i>Size-frequency distribution</i>
decreasing	constant	negative skewness
constant	decreasing	positive skewness
constant	increasing	flattening of curve, possibly negative skewness
constant	constant	mirror image of living population by dead population

Growth-rate and mortality-rate complement each other when one decreases and the other increases, but cancel each other if both increase or decrease.

Higher mortality-rates which favour large populations may result from a fluctuating environment (Valentine 1971). Mortality is affected by nutrients, temperature, and salinity changes. In general, invertebrates have higher mortality-rates in the early stages of life, but the rate may be lower in some species than others (Craig & Oertel 1966). Environmental conditions in estuaries and lagoons would be expected to fluctuate widely and rapidly. They would be expected to show a variable salinity range due to evaporation and influx of fresh water, and a high diurnal temperature range. Furthermore, seasonal upwelling of cold water along the Cape west coast leads to marked instability of the environment on the open coast too.

Although growth-rate is an important factor in this type of study, it is one of the attributes about which there is little information. There is evidence, however, that most bivalves maintain a slightly decreasing, but nearly linear, growth-rate throughout life (Craig & Oertel 1966). This has been shown to be the case for *Cardium edule*, *Tapes japonica*, *Dosinia exolata*, and *Venus striatula* (Kristensen 1959; Wilbur & Yonge 1964).

The most likely effect of the unstable environmental characteristics of the west and south coasts of the Cape would be a high mortality-rate among the juvenile molluscs. Assuming a constant growth-rate for the bivalves, the interplay of mortality-rate and growth-rate should lead to a positively skewed size-frequency distribution for a life assemblage, or an indigenous death assemblage.

Besides the effect of growth-rate and mortality-rate on the shape of the histogram, the assemblage may be affected by post-death mechanical change such as sorting or winnowing by currents (Boucot 1953) and selective fragmentation, and solution of the smaller or thinner shells. Experience with the west coast fossils shows that crushing and fracturing is of primary importance, and affects the bivalves more than the gastropods.

The large number of fragmented shells in both the open-coast facies and estuarine-lagoonal facies sediments suggests death assemblages that have undergone considerable modification by wave-action. Whereas the open-coast bivalves are usually disarticulated, those in the estuarine-lagoonal sediments show a high degree of articulation. These sheltered embayment sites contain epifaunal and infaunal molluscs, some of which are preserved in their living positions. Size-frequency distributions for some of the bivalves are shown in Figure 2. Since the warm-water element inhabited the Late Pleistocene lagoons and estuaries, samples from those environments have been analysed in most detail.

A single sample from a known high-energy open-coast site was examined in detail. Figure 2A shows the size-frequency distribution for *Venerupis senegalensis* from the Velddrif site. The field-setting suggests a transported death assemblage in which vigorous wave-action piled shell debris up to form a breaker-bar. In these deposits the thinner shells have generally been fragmented. The *V. senegalensis* population is composed of thick-shelled forms. Its estuarine ecomorph, on the other hand, has a thinner shell and is of more constant morphology. The Velddrif *V. senegalensis* shows marked negative skewness ( $-0,82$ ). It has an articulation ratio less than 0,05. Articulation ratio is defined as the ratio of complete shells/ $\frac{1}{2}$  (RV+LV).

Size-frequency distributions of bivalves from the estuarine-lagoonal facies differ from the pattern of the Velddrif example. *Tellina madagascariensis* from Verlorevlei (Fig. 2C) and Churchhaven (Fig. 2H) tends to have a flattened histogram. The Verlorevlei *Tellina* has a size-peak at 64–66 mm, and the Churchhaven specimens at 56–60 mm. While the narrower size range of the Verlorevlei material (50–86 mm) suggests a transported death assemblage, the greater range of the Churchhaven material (16–74 mm; more juveniles) suggests an indigenous death assemblage. That this argument can be misleading is shown by their articulation ratios of 1,46 and 0,47 respectively. At both of these localities *T. madagascariensis* is associated with comminuted shells and disarticulated valves of other species. *T. madagascariensis* at Verlorevlei was observed in a nearly horizontal attitude as were the other bivalves. But whereas

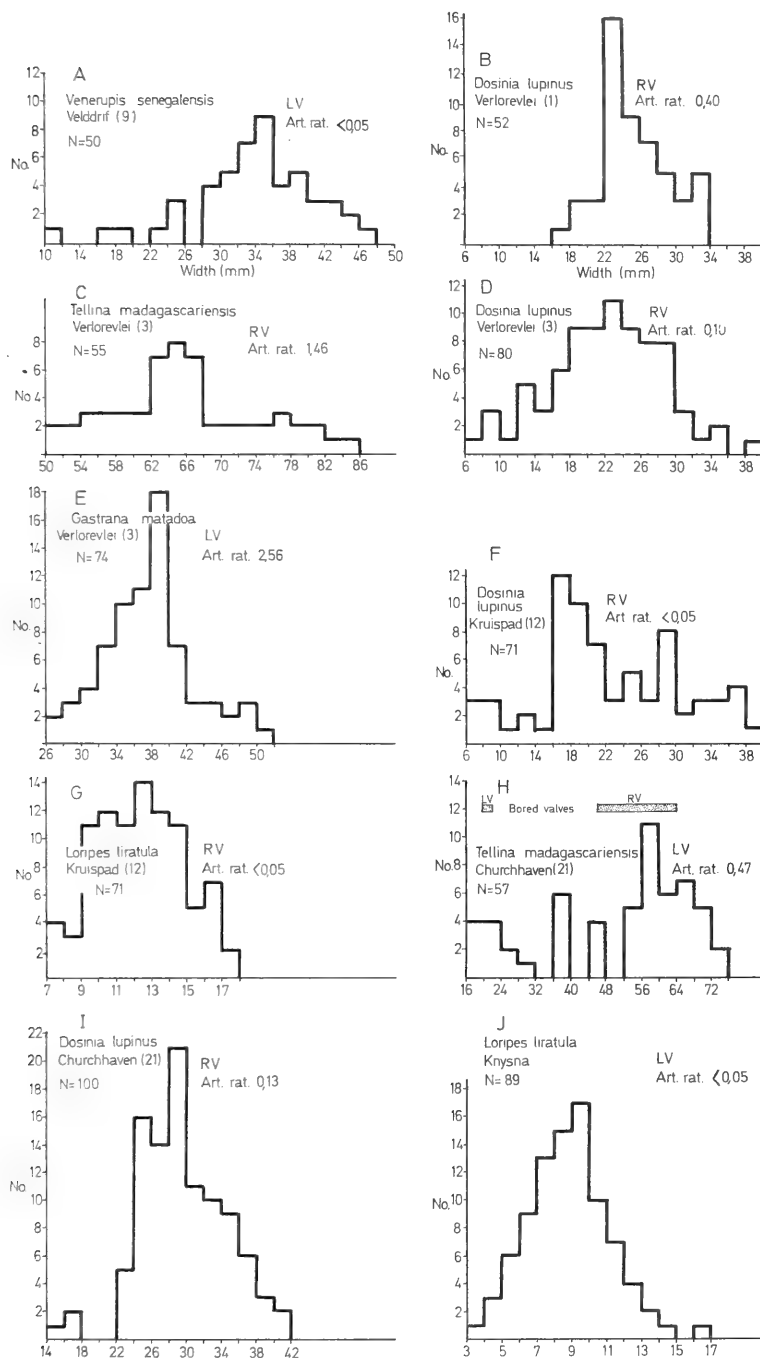


Fig. 2. Size-frequency distribution of selected bivalve shells.

most bivalves burrow with the shell vertical, *Tellina* burrows rapidly and settles in a horizontal position. For this reason the posterior end of the shell is strongly flexed to the right so as to broaden the radius of curvature of the siphons to minimize the current flow constriction. In a small quadrat at Verlorevlei 29 articulated shells were observed. Of these 26 had the right valve uppermost, i.e. flexure upwards, and with the posterior end slightly raised. Many of the *T. madagascariensis* shells still had the ligamental material attached across both valves as a powdery residue. Clearly these animals must have died in their life positions where the weight of sediment prevented opening of the shells after relaxation of the adductor muscles. If they had opened after death and subsequently closed again due to increased sediment load, the ligament would have broken.

At Verlorevlei the *T. madagascariensis* (site 3) size-frequency distribution can be compared with those of *Gastrana matadoa* and *Dosinia lupinus* (Fig. 2B, D, E). *Dosinia lupinus* at site 1 (Fig. 2B) has a positively skewed (+0,37) histogram with an articulation ratio of 0,40. The field occurrence suggests that reworking of the sediment has taken place, although the shells are still situated close to their original life habitat. Although the articulation ratio is high, relative displacement of each valve is common. At site 3 the *D. lupinus* histogram is bell-shaped (Fig. 2D). Here the articulation ratio is only 0,10. The bell-shaped distribution suggests less winnowing of the small specimens. Both *D. lupinus* populations peak at 22–24 mm. From site 1 to site 3 at Verlorevlei there is a tendency for a greater spread of size-ranges of *D. lupinus*: 16–34 mm at site 1 and 6–40 mm at site 3. Conceivably the histogram for *D. lupinus* (site 1) was originally bell-shaped but winnowing may have removed the smaller sizes. This is borne out to an extent by the increase in relative proportions of *Loripes liratula* in the assemblage, from 9 per cent at site 1 to 26,4 per cent at site 3. The size-range of *L. liratula* 3–17 mm (Fig. 2G, J) coincides with the juvenile fraction of *D. lupinus*. Because of the close similarity in shape of *D. lupinus* and *L. liratula*, equal-size specimens of each species would be expected to be hydraulically equivalent.

The size-frequency distribution of *Dosinia lupinus* at Churchhaven has a tail towards the larger specimens (Fig. 2I), suggesting winnowing. It has a narrow size-range, 14–42 mm, and peaks at 28–30 mm. The low articulation ratio (0,13) suggests reworking.

At Kruispad the *Dosinia lupinus* population again has a wide size-range, 6–40 mm (Fig. 2F), but an articulation ratio less than 0,05. Furthermore, the histogram has two peaks, at 16–18 mm and 28–30 mm. The bimodal distribution could be explained by extinction of one living population, followed by fresh recruitment when environmental conditions improved. The site is 15 km up the Berg River and could possibly have been influenced by sudden influxes of fresh water. But *Loripes liratula* at this site appears to represent a single population: the histogram is bell-shaped and peaks at 12–13 mm. Its low articulation ratio (< 0,05) may be meaningless since this species does not have prominent



dentition, and seldom in this study were articulated valves encountered. For example, *Loripes liratula* from Knysna has an articulation ratio less than 0,05 although juveniles dominate. Craig (1967) found that of five species he examined, only *Divaricella quadrisulcata* tended toward a normal distribution. (*Divaricella* and *Loripes* are both Lucinidae.)

*Gastrana matadoa* (Fig. 2E) at Verlorevlei is positively skewed and has a high articulation ratio (2,56). This high articulation ratio, compared with that of *Dosinia lupinus* from the same site, could be due to the more robust dentition of the former, but the greater proportion of juveniles of *G. matadoa* suggests it probably is closer to a life assemblage.

In general, the sign of skewness alone as used by Boucot (1953) is insufficient to distinguish between indigenous and transported death assemblages. The field-setting shows the Velddrif breaker-bar deposit to contain a transported death assemblage. It has strong negative skewness and a low articulation ratio. This tail towards the left has been produced by winnowing of the finer fractions, and effectively displacing the mode towards the coarser size-grades. The other size-frequency distributions are suggestive of indigenous death assemblages which have in most cases been slightly reworked. In Figure 2B the lack of juveniles of *Dosinia lupinus* coincides with low numbers of the hydraulically equivalent *Loripes liratula*.

Other indications that the shells are found in the sediment in which they once lived include relatively high articulation ratios of the larger shells. Smaller shells, e.g. *Loripes liratula*, tend to have weaker hinge attachments, while juveniles of other species may have been subjected to predation. *Tellina madagascariensis* at Verlorevlei appears to be in a life orientation, and also has the ligamental material still attached. At Kruispad a bed contains *Panopea glycymeris* still in the life orientation. The shells were all articulated, all posterior end upwards, and all on the same horizontal plane, i.e. they had all burrowed a siphon-length below the sediment-water interface. At most sites, left and right valves were present in equal proportions.

In conclusion, the field-setting shows that open-coast assemblages are all transported death assemblages, but transportation has been only local. The faunas of the sheltered environments are mixed life and indigenous death assemblages. Taken as a whole the fauna of the open-coast facies and the estuarine-lagoonal facies are consistent with the inferred Late Pleistocene environments.

#### PREDATION

Many of the bivalve shells are punctured by countersunk borings, 1–2 mm in diameter, made by predatory gastropods. The bored bivalves include: *Dosinia lupinus*, *Tellina madagascariensis*, *Gastrana matadoa*, *Venerupis senegalensis*, *Venerupis dura*, and *Ostrea algoensis*. *Crepidula capensis* and *Natica genuana* were the most frequently bored gastropods.

At Churchhaven 17 per cent of *Dosinia lupinus* and 17 per cent of *Tellina*

*madagascariensis* were bored. In the case of the former an equal number of right and left valves were bored, as would be expected in view of the fact that it burrows in a vertical position. Analysis of predation on *T. madagascariensis* reveals a very different pattern. Successfully bored valves fell into two size-classes (Fig. 2H). The first group comprised juveniles with a size range 20–22 mm, and the second group adults with a size range 46–64 mm. Only right valves of adults were bored, which is to be expected because this species lives buried in sediment in a horizontal position and with right valve uppermost. Craig (1967) found that the right valve of *Tellina radiata* was also preferentially bored. The second group of *T. madagascariensis* comprised juveniles in which left valves were preferentially bored, although a few right valves were also bored. The preferential boring of juvenile left valves could also be the result of the burrowing characteristics. *Tellina* is a rapid burrower (Stanley 1970). Depth of burrowing would be controlled by length of the siphons, and for this reason the juveniles would presumably live at shallower depths than the adults and would possibly burrow more slowly. Subsequent current scour would possibly reach only the juveniles and flip them over to leave them left valve uppermost. This also suggests that, besides predation, the juvenile bivalves would be more susceptible to environmental changes since they live closer to the surface.

Most of the bored bivalve shells have only one hole, which is not surprising since only one puncture is necessary to kill the animal. In a few cases two holes per shell were encountered. As far as *Tellina madagascariensis* is concerned the borings occur most frequently in the antero-dorsal half of the shell (Fig. 3). It was also observed that all bored specimens of *T. madagascariensis* at Churchhaven consisted of separate valves, while four bored articulated shells of *Dosinia lupinus* were observed.

Of the gastropods, *Crepidula capensis* was the most extensively bored. Again there was usually only one hole per shell, although up to three were recorded. The reason why *Crepidula capensis* is so susceptible to predation is because it lives exposed at the surface where it is an easy prey. Unlike the bivalves, *Crepidula* does not appear to have any preferred area for boring (Fig. 3).

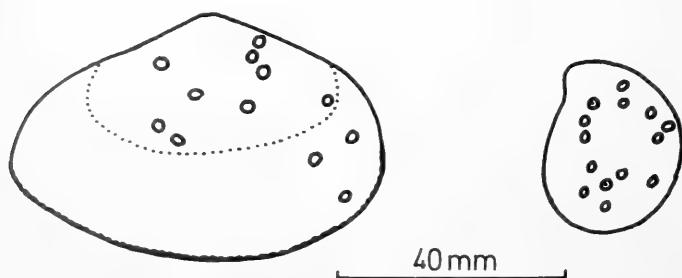


Fig. 3. Predation: distribution of borings on *Tellina madagascariensis* (left), and *Crepidula capensis* (right).

*Crepidula capensis* from the shell beds north of Laaiplek have smaller bored holes (less than 1 mm) than other *C. capensis* or the bivalves.

It is difficult to isolate the species that would have been the predator, although it seems probable that the borings were made by a gastropod. The most likely predator would appear to be the buccinid *Burnupena papyracea*. Where many bivalves were found to be bored at Churchhaven, *B. papyracea* was very prominent. At Verlorevlei there was a total absence of *B. papyracea* and no sign of predation on bivalves.

#### TERATOLOGICAL SPECIMENS

Teratological specimens are those that are outside the normal range of variation of a species (Ager 1963). At most sites an occasional aberrant form was observed, and it was found generally that *Gastrana matadoda* was the most susceptible to damage during life. This was very apparent at Verlorevlei (site 3) where 27 per cent of *G. matadoda* were in some way deformed, compared with less than 2 per cent for *Tellina madagascariensis*. Perhaps this reflects the degree of adaption of *G. matadoda* to its niche, and that the environment at Verlorevlei in particular did not favour this species.

#### DEPTH

Regional geomorphic analysis suggests that the depth of water reflected in the strata of all open-coast and sheltered embayment sites examined could not have exceeded 5 m. The Late Pleistocene estuarine-lagoonal facies is dominated by intertidal deposits, and the open-coast facies by beach deposits. At Velddrif there is a good exposure of a breaker-bar with a washover-fan the top of which is probably a close approximation to high water spring tide. At Churchhaven and Kraalbaai *Callianassa* burrows and crab-burrows are still preserved, indicating an intertidal or shallow subtidal environment. The ostracod fauna, too, is indicative of intertidal conditions.

Very few of the 124 species listed in Table 1 suggest water depths greater than 25 m. Most of these species live today in intertidal and the uppermost sublittoral zones. Less than 4 per cent of the fauna lives today in water deeper than 25 m.

Of the open-coast assemblages *Nassarius speciosus* is today usually dredged, although it is sometimes found intertidally. No more than a few isolated shells were found. *Erycina subradiata* has been encountered at 26 m (Barnard 1964). Other species have a wide depth range although they are common in the intertidal zone. Nearly all species of *Patella* encountered at open-coast sites are intertidal. Only *P. miniata*, *P. tabularis*, *P. compressa* are infratidal (Branch 1971). Other intertidal molluscs include: *Littorina knysnaensis* (above HWN), *Marginella capensis* (low tide down), *Bullia digitalis* (follows the tide), *B. laevis*, *Thais cingulata*, *Burnupena papyracea* (below mid-tide), *Perna perna* (mid-tide), *Aulacomya ater* (mid-tide to low tide on rocky shores), *Choromytilus meridionalis*, *Dosinia lupinus*, *Donax serra* (burrows in surf beaches below

mid-tide), *Venus verrucosa* (found on the surface at mid-tide). Depth ranges are given by Day (1969).

Of the estuarine-lagoonal facies molluscs *Ostrea algoensis* prefers depths of 25–200 m, *Tellina ponsonbyi* prefers off-shore waters to depths of 95 m, and *Theora alfredensis* has been dredged from depths below 70 m (Barnard 1964). *Ostrea algoensis* and *Theora alfredensis* are common in this facies. Only one *Tellina ponsonbyi* valve was found at Churchhaven, suggesting that this specimen strayed into shallow water.

Most of the sheltered-embayment molluscs prefer very shallow or intertidal water. These include the gastropods *Patella* spp., *Littorina knysnaensis* (HWN), *Turritella capensis* (quiet water shallower than 3 m), *Oxystele variegata*, *Burnupena papyracea*, *Nassarius kraussianus* (mud-banks and weed-beds of estuaries); the bivalves *Loripes liratula* (muddy sand at low tide), *Solen capensis* (muddy sand of estuaries), *Venus verrucosa*, *Choromytilus meridionalis*, *Perna perna*, *Aulacomya ater*, *Tellina madagascariensis* (extensive infratidally), *Dosinia lupinus*, *Donax serra* and *Panopea glycymeris*.

None of the constituents of the open-coast or estuarine-lagoonal facies required water depths greater than about 25 m. Modern bathymetric ranges for the species suggests maximum Late Pleistocene water depths at these sites of the order of 0–5 m. This is consistent with the geomorphic evidence.

#### TEMPERATURE

Since the primary purpose of this paper is a discussion of a southerly migration of tropical and subtropical mollusc species in the last interglacial, the most important criteria are those indicative of temperature. Sea surface temperature inferences may be made by comparing geographic ranges of living molluscan species with those of their fossil counterparts. Although the fossil fauna of the west coast is distinctly modern in character, the estuarine-lagoonal facies assemblages regularly contain several species whose present-day distribution is restricted to tropical and subtropical waters. The modern geographic range end-points of the thermophilic species that live further north on the west African coast are separated by 2 000 km from the fossil occurrences in the south-western Cape, so that the fossil assemblages contain species that do not today live in association. Northward migration of the extralimital species was probably induced by deteriorating environmental conditions. Since the geographic ranges of recent molluscs seem to be determined mainly by temperature (Valentine 1955), it would appear that falling temperature was the compelling factor. It could also be argued that lower temperatures accompanied the advance of the Weischelian ice-sheets, in which case falling sea level would have drained the Late Pleistocene estuaries and lagoons. But with reflooding of these environments in Recent time, the thermophilic molluscs did not return.

Mollusc assemblages in the estuarine-lagoonal facies of the west and south coasts contain a total of more than 20 species that do not sustain populations in those areas today. West coast sites contain 15 such species,

TABLE 2  
Present-day Geographic Ranges, Temperature Minima, and Distribution of some Fossil Molluscs  
*Fossil Assemblages*

TABLE 2 (contd.)  
Present-day Geographic Ranges, Temperature Minima, and Distribution of some Fossil Molluscs

	COLD WATER TAXA	Fossil Assemblages			
		W. Coast		S. Coast	
		Minimum Temp. °C*	Open	Estuaries, Lagoons	Knysna
<i>Temp. range</i>					
GASTROPODA		14-17	×	×	
	<i>Thais cingulata</i>	14-17	×	×	
	<i>Burnupena papyracea papyracea</i>	14-17	×	×	
	<i>Nassarius plicatellus</i>	14-17	×	×	
	<i>N. scopularcus</i>	14-17	×	×	
	<i>Conus scitulus algoensis</i>	13-17	×		
BIVALVIA					
	<i>Tellinomya trigona</i>	12-16		×	×
	<i>Lutraria lutraria</i>	12-15	×	×	

mainly bivalves. These extralimital molluscs, their present-day geographic ranges, and minimum temperature tolerances are shown in Table 2.

It is often difficult to assess the minimum temperature tolerance of living molluscs. Zinsmeister (1974) divides the normal biogeographic range of a taxon into a spawning range, and a non-spawning range. The modern geographic range of *Ostrea atherstonei*, from Saldanha to Bushmans River, implies a minimum temperature tolerance of about 13°C. But it appears that present temperatures in Saldanha Bay are too low for spawning (Korringa 1956). Spawning experiments in this area have confirmed this, and suggest that the oyster larvae may actually originate in an area of higher water temperature. It is possible that several species of molluscs extend their geographic range end-points by inhabiting local pockets of warm water such as estuaries. If this is the case then the temperature minima shown in Table 2 may actually be too low. It is not always clear from the literature whether the range end-points are open-coast, estuaries or embayments. Other difficulties arise from taxonomic problems. For instance, *Macoma ordinaria* and *M. crawfordi* may be geographic variants of the Mediterranean *M. cumana*.

#### 1. West coast estuarine-lagoonal facies

Because of physiographic changes at Verlorevlei and the lower reaches of the Berg River, present temperature ranges would be meaningless standards against which to measure Late Pleistocene changes. The present shoreline of Langebaan Lagoon has changed little since the last interglacial, and present temperatures at Churchhaven could be used as an approximation for the other sites as well. Day (1959) gives a surface temperature range for Churchhaven of 13,5°C to 37°C (HW) and 38,5°C (LW).

The fossil assemblage at Verlorevlei (site 3) is represented by 23 species of molluscs, 6 of which are indicative of warm water. These 6 thermophilic species constitute 42 per cent of the total individuals. The modern geographic range of *Loripes liratula* (26,4 per cent of the fauna) is Mauritania to Angola (Nicklès 1950), where its minimum temperature requirement would be 17–18°C. *Ostrea stentina* (2,7 per cent), *Tellina madagascariensis* (8,1 per cent), *Macoma tricostata* (< 1 per cent), and *Venerupis dura* (< 1 per cent) are also tropical west African species and could not tolerate temperatures below about 17°C. *Gastrana matadoa* (4,1 per cent) extends into water as cool as 14°C. Accepting that stenothermal organisms are more critically limited by minimum temperatures than by maximum temperatures (Durham 1950), it would appear that the minimum temperature in this Late Pleistocene estuary must have been 17–18°C, or at least 3°C warmer than present Churchhaven surface temperatures.

At Kruispad (site 12) 8 of the 31 species prefer warm water, and constitute 47,9 per cent of the total individuals. Of these *Nuculana bicuspidata* (3,2 per cent), *Loripes liratula* (15,4 per cent), and *Leporimetis hanleyi* (1,0 per cent) have a minimum temperature requirement of 17–18°C. A significant constituent of this assemblage is *Panopea glycymeris*. Although it forms less than 1 per cent

of the total individuals, it is nevertheless very common (because it is a large animal, about 200 mm, and is always found in life orientation, a shell count in a 1 m quadrat would be unlikely to yield more than one or two specimens). *Panopea glycymeris* lives in areas with a temperature range 20–27°C (Kensley 1974), although it could probably tolerate cooler water. This assemblage is thus indicative of a temperature minimum of about 18°C. At Bloemendal (site 11) *Loripes liratula* and *Leporimetis hanleyi* are common.

Three sites examined along the shore of Langebaan Lagoon yielded a significant proportion of thermophilic molluscs: Geelbek (site 19; 7 species in 26 constituting 46,0 per cent of the fauna), Skrywershoek (site 20; 6 species in 19 constituting 32,9 per cent of the fauna), and Churchhaven (site 21/22; 7 species in 31 constituting 28,1 per cent of the fauna in the lower unit; 7 species in 27 constituting 35,5 per cent of the fauna in the upper unit). The dominant thermophilic mollusc content at these sites is as follows:

	Geelbek	Skrywershoek	Churchhaven	
			Lower	Upper
	%	%	%	%
<i>Ostrea atherstonei</i>	5,1	7,1	1,0	5,0
<i>Loripes liratula</i>	20,4	14,1	1,0	4,1
<i>Macra ovalina</i>	1,0	1,2	2,3	1,7
<i>Tellina madagascariensis</i>	10,2	9,4	23,4	3,3
<i>Leporimetis hanleyi</i>	—	< 1,0	—	—
<i>Venerupis dura</i>	4,1	1,2	—	—

All of these species, except *Ostrea atherstonei* and *Macra ovalina*, have a minimum temperature requirement of 17°C. *Ostrea atherstonei* is found living today in Saldanha Bay, but temperatures are apparently too low for spawning. It is possible that this species has a minimum temperature tolerance of 14°C. The floor of the present lagoon is underlain by about 3 million metric tons of *O. atherstonei* shells, with little detrital sediment, suggesting optimum temperatures for breeding, and hence probably greatly in excess of 14°C. *Macra ovalina* has a minimum requirement of 19°C. A minimum temperature in the Late Pleistocene lagoon of about 18°C is indicated, about 4–5°C warmer than the present surface temperature minimum at Churchhaven.

## 2. South coast estuarine—lagoonal facies

A Late Pleistocene site at Knysna was the only one on the south coast examined in detail. But examination of material in collections of the South African Museum shows that very similar fossil faunas exist at Sedgfield, and Groot Brak and Klein Brak estuaries. The fossil assemblage at the Klein Brak estuary contains *Panopea glycymeris*, but their shells are, on average, much smaller than the Kruispad specimens (Kensley 1974).



The Knysna assemblage contains 47 molluscan species, of which 6 are extralimital and which constitute 60,4 per cent of the individuals. But these 6 species include the extinct subspecies *Cantharidus suarezensis fultoni* (9,8 per cent) and *Cerithium scabridum rufonodulosum* (16,3 per cent). Although the geographic ranges of the species is shown in Table 2, it is obviously not certain that the extinct subspecies had the same temperature tolerances. Their Recent relatives *Cantharidus suarezensis suarezensis* and *Cerithium scabridum* have minimum temperature requirements of 19°C and 24°C respectively. *Alys cylindrica* (< 1 per cent) has a minimum temperature requirement of 21°C. Of the bivalves *Felania diaphana* (3 per cent), *Tellina madagascariensis* (< 1 per cent), *Leporimetis hanleyi* (< 1 per cent) and *Venerupis dura* (< 1 per cent) all suggest temperature minima of 17°C. *Loripes liratula* (57,5 per cent) also suggests a temperature minimum of 17°C, but the fact that it occurs in such great numbers, and the fact that all growth stages are present (Fig. 2J), suggest optimum conditions. Together the evidence suggests a temperature minimum in excess of 17°C for the Late Pleistocene estuary. Day *et al.* (1952) gives a temperature range at the railway bridge of 12–24°C.

### 3. West coast open-coast facies

The present-day temperature range on the adjacent open coast is about 13–15°C (Shannon 1966). The fossil assemblage contains only three species which prefer warm water, but which never constitute more than 1 per cent of any assemblage: *Cypraea algoensis*, *Marginella piperata* and *Scissodesma spengleri*. The marked paucity of warm-water species indicates that Late Pleistocene nearshore water temperatures were not very different from the present.

### SUMMARY

Before discussing the palaeoclimatic significance of the extralimital molluscan species it may be as well briefly to summarize the evidence.

1. All fossiliferous Late Pleistocene estuarine-lagoonal facies deposits contain extralimital species which usually constitute more than 30 per cent of the individuals of each assemblage, and which indicate minimum water temperatures 4–6°C warmer than the present-day estuaries and lagoons, with minimum temperatures of about 18°C. Kanakoff & Emerson (1959) suggest temperatures in excess of 19°C for similar Californian occurrences.

2. All growth stages of the thermophilic molluscs are present (Fig. 2). The importance of this is that it implies that temperatures were such that the normal spawning range of each mollusc is represented. Normal spawning range is characterized by a population which continually maintains its numbers (Zinsmeister 1974). The large number of individuals and presence of all growth stages show that the thermophilic taxa formed self-sustaining populations that were adequately adapted to the depositional environment.

3. The estuarine-lagoonal facies contain mixed life and indigenous death

assemblages of molluscs. These molluscs obviously lived in environments reflected in the sediments, and have suffered little post-death transportation.

4. The sediments and their mollusc fossils indicate water depths in general less than 5 m.

5. The fact that sediments with high proportions of extralimital molluscan species characterize most Late Pleistocene estuary and lagoonal situations, that these molluscs formed self-sustaining populations and inhabited very shallow water, suggests that the marine transgression to 6 m in the last interglacial was a major event during a climatic optimum.

Zinsmeister (1974) has suggested that similar, well documented occurrences of thermophilic molluscs in Californian Late Pleistocene embayments represent only temporary, non-breeding, members of the community. He believes that periodic local and temporary current changes introduced tropical mollusc larvae into areas of cooler water, and that these molluscs represent only temporary members of the community since temperatures would have been too low for them to maintain self-sustaining populations.

Zinsmeister's arguments stem from the fact that previous studies paid scant attention to the population dynamics, and consequently they fail to prove the presence of self-sustaining populations. Similar occurrences in the south-western Cape support the view that these faunas are the result of a warmer climate which must have affected the whole world. Age-wise these deposits are also similar and probably coincide with a high climatic peak (substage 5e) and sea level up to 7 m higher than present at 120 ka (Shackleton 1969).

6. Configuration of the coastline was probably very important. Today a low Palaeozoic rock bar just above high-tide level keeps the sea out of Verlorevlei. A slight rise of sea level would create radical changes at Verlorevlei. Likewise the lower reaches of the Berg River formed a prominent estuary due to flooding by last interglacial high sea levels. Normally one would expect to find an overlap of geographic ranges of tropical and temperate species. In an overlap area the tropical species would be restricted to inshore, protected environments, and temperate species would live in the cooler open coast sites (Emerson 1956).

## PALAEOCLIMATIC INTERPRETATION

### REVIEW OF PRESENT CLIMATE AND HYDROLOGY

The south-western Cape has a Mediterranean-type climate. Hot, dry summers are the result of the dominant anticyclones in those months, while depressions associated with westerly winds bring rainfall in winter.

Hart & Currie (1960) have summarized the effect of the wind system on the climate of the south-western Cape Province. A subtropical high-pressure system is centred between 26° and 30°S. To the south this high-pressure system borders on the 'westerlies' causing a steep pressure gradient. The south-easterly winds of the south-western Cape are the result of winds blowing anticyclonically

around this high-pressure system. In summer the centre of the anticyclone lies at about 30°S and brings strong south-easterly winds to the south-western regions, but in winter it moves northwards to 26°S. The westerly wind system follows the anticyclone northward and the southern Cape is then frequented by depressions which bring rain from the south-west Atlantic, although the Namib Desert is still influenced by the Trade Wind belt.

The west coast of southern Africa, like the west coasts of other countries in similar latitudes, is characterized by a linear belt of centres of upwelling of cold subsurface water (Central Water) from Lüderitz to the Cape Peninsula (Fig. 1 insert). There is a north-south isotherm lineation with the coldest and least saline water near the coast (Shannon 1966). This upwelling, the Benguela Current, varies in intensity depending upon the wind system and local topography. The upwelling phenomenon arises from the displacement of surface water northwards and off-shore by the south-easterly wind system. Cooler subsurface water wells up to replace this warmer water. The result of this active upwelling is a complex system with tongues of cold water alternating with intrusions of warmer oceanic waters, and all diverging to the north-west (Bang 1971). Bang defines the Benguela Current as the area east of a belt of off-shore divergence within which the oceanic processes are dominated by short-term atmospheric interactions.

During the winter months when the anticyclone centre moves northward, weakening of the southerly wind component results in weakening of the upwelling system also. With less upwelling the surface waters over the inner part of the continental shelf are warmer by 2°C, but off-shore a drop in temperature tends to minimize this affect. With weakening of the Benguela Current system and the greater prominence of westerly and north-westerly winds, a southward-flowing inshore counter-current develops. Shannon (1966) mentions a predominantly southward-flowing counter-current between Lambert's Bay and Cape Point which is present during all seasons, but most marked in winter. A southward-flowing counter-current carries 'seeboontjies' from Angola and driftwood from the Orange River southwards (Wagner & Merensky 1928). Surface temperatures at the Orange mouth rise noticeably when the north-westerly winds blow.

The highest surface-water temperatures are encountered in the lagoons and estuaries which are protected from the effects of upwelling. The temperature range in Langebaan Lagoon, 10–39°C (Day 1959), contrasts markedly with that of the near-by open sea, 13–15°C (Shannon 1966). During the summer months temperatures in Langebaan Lagoon are at a maximum, while those of the open sea drop.

The currents off the east and south coasts, the Mozambique Current and Agulhas Current, have been studied by Clowes (1950), Orren (1963, 1966), and Darbyshire (1964). Both of these currents are southward extensions of the great South Equatorial Current which flows westwards across the Indian Ocean. At 26°S the Mozambique Current is met by the southern branch of the South

Equatorial Current, which is divided by Madagascar, and they combine to form the Agulhas Current. The Agulhas Current is finally deflected by the Agulhas Bank (Clowes 1950) (Fig. 1).

Upwelling does take place off Cape Agulhas but it is a geostrophic upwelling, i.e. the upwelling varies with the velocity of the current. Here the Agulhas Current is weakest and Agulhas water retreats northwards in winter, thus allowing Central Water to reach the surface. In summer, when the Agulhas Current is flowing at its strongest, it overrides the Central Water (Darbyshire 1964). Sometimes in summer the warm Agulhas Current moves away from the south coast and allows cold Central Water to replace it inshore, and within a day or two the temperature may fall by as much as 10°C (Day 1963). Schell (1968) describes the occasional penetration of the Agulhas Current round the Cape Peninsula into the South Atlantic.

#### LATE PLEISTOCENE CLIMATE

It would be expected that the intensity, and probably position, of the anticyclones would vary with the solar radiation. A climatic optimum at 120 ka produced temperatures warmer than at any other time in the last 120 ka (Shackleton 1969). The anticyclone would have moved south of latitude 30°S (Van Zinderen Bakker 1967: fig. 6). This would lead to the linear west coast upwelling belt moving south in response, and the winter-rainfall area would be more strictly restricted to the south-western Cape. Such a southward movement would be accompanied by more pronounced upwelling off the west coast than at present, and would operate over a longer period of time just as happens on the Namib Desert coast. Since the Central Water originated in the Southern Ocean, and since the Antarctic ice-sheet was essentially stable throughout the Pleistocene (Mercer 1968), it is unlikely that the upwelling water would have been any colder than the present. This is confirmed by the fossil molluscs from the open-coast facies which suggest little temperature change. Addicott & Emerson (1959) and Valentine (1955) have also suggested intensified nearshore upwelling and a poleward expansion of isotherms to explain their mollusc faunas.

Eustatic rise of sea level would have changed the configuration of the coast by forming salt-water estuaries at Verlorevlei and the Berg River, as well as at numerous sites along the south coast. The present coast is not as embayed as the Late Pleistocene coast would have been. Thermally anomalous assemblages existed contemporaneously only in the vicinity of the protected bays where the increased solar radiation of the last interglacial heated the surface water considerably.

Periodic current changes permitted the introduction of tropical mollusc larvae into these pockets of warm water. The intensification of atmospheric circulation that led to more pronounced upwelling presumably also affected the inshore counter-current which possibly flowed more strongly than at present. Isaacs & Sette (1959) described anomalous wind fields in the Pacific area during

1957 and 1958 which so changed the oceanic circulation that tropical taxa were found far north of their expected ranges. This demonstrates that circulation changes as proposed in this paper do happen at present, albeit less frequently and less pronounced than is here suggested.

On the east coast with intensification of the air circulation intensification of the present summer conditions would also be anticipated. Presumably the Agulhas Current flowed more strongly than today and continually overrode the Central Water, perhaps with frequent eddies of Agulhas water around the Cape Peninsula. This would limit the likelihood of sudden incursions of cold water, such as presently affect the Knysna estuary in summer and cause temperatures to drop between 10 and 15°C (Korringa 1956).

These possible changes in the oceanic circulation during the hyperthermal period would have had far-reaching effects on the distribution of molluscs. Because of the low migratory ability of molluscs in the post-larval stage, their geographic distribution depends primarily on the dispersion of larvae. Distribution of the planktonic larvae depends upon ocean currents. About 85 per cent of tropical marine molluscs have a free-swimming pelagic larval stage which can exist, on average, three to four weeks before settling (Zinsmeister 1974). Dietrich (1935 in Korringa 1956) gives the velocity of the Agulhas Current as 50 km per day. At this rate larvae could be transported 1 000 km before metamorphosis. Larvae can apparently withstand sudden changes of temperature; Korringa mentions a change from 25° to 2°C which did not adversely affect oyster larvae.

A general southward movement of isotherms on the west and south coast is envisaged. This would have brought the tropical mollusc zone closer to the south-western Cape. Periodic expansions of the warm-water isotherms coupled with an intensified inshore counter-current on the west coast would have enabled tropical mollusc larvae to pass the cold Benguela barrier. If the larvae reached the sheltered estuaries and lagoons of the south-west coast, increased solar heating (substage 5e) would have allowed these molluscs to sustain their populations and persist there even after the open-coast thermal barrier became impassable again. Those thermophilic larvae that reached metamorphosis on the open coast may well have survived, but there is no evidence that they were able to sustain their populations. South coast estuarine facies show that larvae from the tropical west African coast were able to pass the Cape Peninsula: e.g. *Tellina madagascariensis*, *Loripes liratula*, *Leporimetis hanleyi*, *Venerupis dura*, *Panopea glycymeris*. The Agulhas Current was also able to transport Indo-Pacific mollusc larvae around the Peninsula to the west coast sites. In these sheltered embayments warm-water taxa survived as relicts.

## DISCUSSION

The occurrence of thermophilic molluscs in Late Pleistocene sediments of the south-western Cape far beyond their present-day geographic range end-points is not unique. Similar occurrences in California have been extensively

studied, and the same conditions appear to have operated in the Miocene where the configuration of the coastline was very different from the present. The San Joaquin basin was a protected embayment in the Late Miocene, and there relict faunas persisted long after the temperate faunas had spread southward along the open coast (Addicott & Vedder 1963). The thermally anomalous Late Pleistocene molluscs also lived in shallow protected embayments (Addicott & Emerson 1959). The only significant point of difference between the two regions is that the open-coast facies of the Cape coast contains molluscs which nearly all live on the adjacent coast, while the Californian open-coast facies contains a fauna that reflects cooler water than the present. Valentine (1955) proposed that during the last interglacial of California upwelling was intensified, while at the same time the warmer water of the sheltered embayments was derived from increased solar radiation. He also suggested a general warming of the oceanic waters by increased solar heating.

The Late Pleistocene estuarine-lagoonal facies of the Cape Province are attributed to a eustatic rise of sea level which changed the configuration of the coast and produced a great number of estuaries where the effects of seasonal upwelling were excluded. A southward movement of the south Atlantic anticyclone at this time shortened the cold-water barrier on the western open coast by causing a southward shift of the Benguela Current, and possibly strengthened the inshore counter-current, so that thermophilic mollusc larvae were able to migrate southwards where they could sustain their populations in the solar-heated estuaries and lagoons. It would appear that the present temperatures are too low for breeding.

This history contrasts with that of the Early Pleistocene when sea temperatures on the open coast were much warmer than at present. The last of these warm-water open-coast episodes is associated with the 45–50 m transgression complex of the Namaqualand coast (Carrington & Kensley 1969). *Striostrea margaritacea* was common on the open coast, forming the so-called 'oyster line' (Haughton 1931). This oyster requires a minimum water temperature of 25°C in summer (Korringa 1956). The 45–50 m transgression complex sediments were probably pre-glacial Pleistocene. Such warm conditions must have been in response to the warmer conditions prevailing in the northern hemisphere, since the Antarctic ice-sheet is thought to have been stable throughout the Pleistocene (Mercer 1968). Warming of the northern hemisphere would have moved the intertropical convergence farther south than even its Late Pleistocene position. This would have moved the South Atlantic anticyclone south, and with it the belt of upwelling, bringing tropical waters down the Namaqualand coast. But *Striostrea margaritacea* is totally absent from Early Pleistocene deposits in the Saldanha area, suggesting that cool water, and upwelling, were still dominant there.

If the model for a southward shift of the anticyclonic system in the last interglacial is correct, then one would expect the opposite trend during the Weischelian. Lamb (1961) suggests that Ice Age circulation was marked by

intensified circulation of the belt of westerlies, and greater mobility in the subtropical anticyclones, which generates upwelling systems such as the Benguela Current. Van Zinderen Bakker (1967, in press) presents evidence to show that during hypothermal periods the influence of the anticyclones and the Benguela Current would have shifted northwards to the equatorial regions. Displacement of the westerlies towards lower latitudes would have expanded the winter-rainfall area of the southern Cape, and would have caused a northerly shift of the Namib Desert. Tankard & Schweitzer (1974) have demonstrated, from Die Kelders cave sediments, that wetter conditions in the Weischelian coincided with a cooler period. Butzer (1973) has found a similar record in the Nelson Bay cave. A northward migration of the belt of westerlies would have resulted in a longer rainy season, if not year-round precipitation.

Finally, this study suggests a possible correlation of the last interglacial deposits of the Cape Province with the Eutyrrhenian of the Mediterranean. Although warping of the Eutyrrhenian shorelines is universal (Richards 1962), Bonifay & Mars (1959) have attempted to restore these shorelines to their original elevations. They attribute the Eutyrrhenian shoreline to a transgression to 2–3 m a.s.l. Chronologically the Eutyrrhenian shoreline and last interglacial shorelines of the south-western Cape appear to be similar.

The *Strombus* fauna of the Eutyrrhenian deposits is characterized by *Strombus bubonius* and other species typical of Senegal and west Africa (Richards 1962) which suggest warmer hydroclimates than today. Like the warm water fauna of the south-western Cape, the *Strombus* fauna can also be attributed to poleward expansion of isotherms, and once in the Mediterranean the molluscs remained a relict fauna which survived in water heated by increased solar radiation.

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6. SYSTEMATIC papers must conform with the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. n., sp. n., comb. n., syn. n., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

*Nuculana (Lembulus) bicuspidata* (Gould, 1845)

Figs 14–15A

*Nucula (Leda) bicuspidata* Gould, 1845: 37.

*Leda plicifera* A. Adams, 1856: 50.

*Laeda bicuspidata* Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (figs 8a–b).

*Nucula largillierti* Philippi, 1861: 87

*Leda bicuspidata*: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

*Holotype*

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach, Port Elizabeth (33.51S, 25.39E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and of date.

## 7. SPECIAL HOUSE RULES

### *Capital initial letters*

- The Figures, Maps and Tables of the paper when referred to in the text  
e.g. '... the Figure depicting *C. namacolus* ...'  
'... in *C. namacolus* (Fig. 10) ...'
- The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names  
e.g. Du Toit but A. L. du Toit  
Von Huene but F. von Huene
- Scientific names, but not their vernacular derivatives  
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.



ANTHONY J. TANKARD  
THERMALLY ANOMALOUS  
LATE PLEISTOCENE MOLLUSCS  
FROM THE SOUTH-WESTERN CAPE PROVINCE,  
SOUTH AFRICA